Sexual Selection in Savanna Millipedes: Products, Patterns and Processes

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ABSTRACT

The polygynandrous mating systems of savanna millipedes are a dynamic combination of simple effective male mating tactics, male behaviours that protect their reproductive investment in females and possibly female choice of high quality males. Sexual selection has led to the evolution of dimorphic characters that aid in courtship and mate acquisition. Differential development between the sexes at the onset of breeding activity leads to changes over the breeding season in the OSR, and a prevalence of alternative male mating tactics. Selection via sperm competition may be responsible for the evolution of diverse and complex male gonopods (BARNETT & TELFORD, this volume) and behaviours such as prolonging the duration of copulation. For a morphologically simple and conservative class of invertebrates, millipedes offer great potential for the study of sexual selection.

RÉSUMÉ

Sélection sexuelle chez les Diplopodes de savane : résultats, modalités et processus.

Les modes polygynandres d'accouplement chez les diplopodes de savane constituent une combinaison dynamique des tactiques d'accouplement simples et efficientes des mâles, des comportements des mâles protégeant leur investissement reproducteur auprès des femelles et d'un choix possible des femelles pour des mâles de grande qualité. La sélection sexuelle a conduit à l'évolution de caractères dimorphiques facilitant les parades et l'accouplement. Le développement différentiel entre les sexes à l'approche de la phase d'activité de reproduction conduit à des modifications de la sex-ratio opérationnelle durant la saison de reproduction et avantage les tactiques alternatives d'accouplement des mâles. La sélection par la compétition pour le sperme peut être responsable de l'évolution de gonopodes mâles complexes et diversifiés (BARNETT & TELFORD, ce volume), ainsi que de comportements tels que celui de prolonger la durée de copulation. Pour une classe d'invertébrés à morphologie simple et conservatrice, les diplopodes offrent un large potentiel de recherche dans le domaine de la sélection sexuelle.

INTRODUCTION

For most higher organisms, males produce a surplus of cheap gametes capable of fertilising an infinite number of females, while females produce a finite number of expensive gametes that require only a single mating for effective fertilisation (BATEMAN, 1948; WILLIAMS, 1966). Because of this disparity in the cost of gamete production, males display indiscriminate mating tactics, mate frequently and compete intensely with rivals, while females often exercise highly selective mate choice.

This fundamental behavioural difference between the sexes is the source of a selective process described by DARWIN (1871) as sexual selection. Sexual selection acts on both behavioural and morphological traits that confer a mating advantage to individuals with the most elaborate variant of the trait. Sexual selection acts in two ways: competition between males for access to females (intrasexual selection); competition between males, usually via display, to be chosen by females (intersexual selection). One or both forms of selection are assumed to be responsible for the evolution of the bright and often elaborate plumage of male birds and the horns and antlers of antelope and deer (DARWIN, 1871; TRIVERS, 1985) as well as numerous other examples of pronounced sexual dimorphism (e.g. ALEXANDER *et al.*, 1979; EBERHARD, 1985). Recently, PARKER (1970) described a form of indirect intrasexual selection, namely sperm competition, in which the sperm of different males compete to fertilise ova from within the female. This process of ejaculate competition has proved to be widespread in both vertebrates (BIRKHEAD & HUNTER, 1990; BIRKHEAD, 1989; GOMENDIO & ROLDAN, 1993) and invertebrates (PARKER, 1970; WALKER, 1980; THORNHILL & ALCOCK, 1983; WAAGE, 1986) with polygynandrous mating systems.

Over the past ten years much research has focused on teasing apart the relative contributions of these selective processes to the evolution of mating systems in general (EMLEN & ORING, 1977; BORGIA, 1979), and more specifically to understanding what determines variation in male and female mating success (BROWN, 1988; CLUTTON BROCK, 1988; GRAFEN, 1988).

The study of animal mating systems aims to describe who mates with who, how often, and why. More specifically, researchers wish to identify the selective pressures responsible for the evolution of sexual dimorphism and differences in behaviour (product), determine potential morphological and behavioural correlates of variation in mating success (pattern), and identify the tactics of mate acquisition and the degree of competition therein (process). In this paper we summarise our work to date on the mating systems of southern African savanna millipedes using the themes of product, pattern, and process. We highlight aspects of the work which deserves further consideration and suggest future directions for the study of millipede mating systems.

PRODUCTS

Morphology

Southern African juliform millipedes display marked sexual dimorphism, with females typically heavier and wider, but not longer than their conspecific male counterparts (TELFORD & DANGERFIELD, 1990, 1993a, b). The ovaries of females are paired structures housed in a common median ovitube that runs from ring 15 to the last podous ring (see BLOWER, 1985; HOPKIN & READ, 1992). Our measures of clutch size for savanna millipedes range from 200-800 ova over a size range of 1.0-20.0 grams (n = 15 species, unpublished data).

A cylindrical body plan is a unifying feature of juliform millipedes. The volume of a cylinder is calculated as: $h.\pi r^2$, where h is the height of the cylinder (body length) and r the radius. If, for example, selection for increased fecundity resulted in a twofold increase in radius the resultant increase in volume could only be matched through a fourfold increase in length. The energetic costs associated with increasing body diameter are probably less than would be associated with increasing body length. Presumably natural selection has acted on female body volume in this way to accommodate the ovary and maximise the number of eggs it can contain.

Body volume is not the only sexually dimorphic character. Millipede legs are longer and broader in males compared to females and have adhesive pads on the tarsal segments. The evolution of this sex difference in morphology probably relates to courtship and copulation (see HOPKIN & READ, 1992). Our observations have shown that males of all taxa (except members of the genera *Calostreptus* and *Chersastus*) walk along the back of the female prior to engaging in copulation. The longer broader legs of males with their adhesive pads presumably aid in this

manoeuvreing and may also function in stimulating sexual receptivity in females. Both natural and sexual selection may have contributed to the evolution of sexual dimorphism in limb structure. Data on sexual dimorphism in *Alloporus uncinatus* together with the probable sources of selection are summarised in Table 1.

TABLE 1. — Sexual dimorphism in *Alloporus uncinatus*. Leg width measured in micrometer units. Significance levels: ***P<0.001. **P<0.01. N.S. = Natural Selection; S.S. = Sexual Selection. Source: Modified from TELFORD & DANGERFIELD (1990).

	Males	Females	t-test	n	Selective Pressure
Body mass (g)	8.0 ± 0.11	8.7 ± 0.13	-4.25***	110	N.S.
Body length (mm)	114.1 ± 0.65	110.7 ± 0.87	3.16**	110	N.S.\S.S.
Body width (mm)	8.9 ± 0.06	9.5 ± 0.08	-6.41***	110	N.S.
Leg length (mm)	5.9 ± 0.10	4.9 ± 0.80	-7.83***	20	S.S.
Leg width (μm)	15.9 ± 0.16	13.4 ± 0.26	-8.18***	20	S.S.

In many sexually dimorphic species, males are typically the larger sex because sexual selection favours larger males for their superior competitive ability in contests with rivals (THORNHILL & ALCOCK, 1983; TRIVERS, 1985). Body design in male millipedes may reflect their greater mobility. Mobility seems to be an important determinant of mate acquisition (see Behaviour section below) with both longer legs and longer body resulting in males being able to move more quickly and efficiently than females. This idea remains to be tested.

TABLE 2. — Sex differences in the behaviour of three species of juliform millipede expressed as the percentage of the total number of observations (values in brackets). Expected frequencies for between sex comparisons are based on the overall sex ratio for the species and the total number of observations in the behaviour category. Source: modified from DANGERFIELD, MILNER & MATTHEWS, (1992).

	Walking	Feeding	Resting	Copulating
Calostreptus carinatus				
males (62)	64.5	11.3	9.7	14.5
females (223)	25.1	34.1	36.8	4.0
χ^2	22.0***	8.6**	10.9***	8.4*
Chaleponcus digitatus				
males (148)	66.2	23.0	10.1	0.7
females (212)	34.9	42.0	22.6	0.5
χ^2	17.5***	9.7**	7.9**	0.1ns
Alloporus uncinatus				
males (86)	69.8	18.6	3.5	8.1
females (158)	47.5	40.5	7.6	4.5
χ^2	4.9*	7.9**	2.6ns	1.3ns

Behaviour

Savanna millipedes are surface active during the summer wet season and, depending on habitat and rainfall patterns, may remain active for as long as six months (DANGERFIELD & TELFORD, 1991; DANGERFIELD, MILNER & MATTHEWS, 1992; TELFORD & DANGERFIELD, 1993a). During this period adults, intercalary males and juveniles emerge from underground to feed and reproduce. Significant differences between the sexes are apparent in the time invested in the performance of these behaviours as well as in their general activity patterns (Table 2). For example, in a population of *Alloporus uncinatus* from Mazowe, Zimbabwe (17°30'S, 30°57'E) males were more active than females, who spent more time feeding in aggregates, and climbing vegetation; apparently to avoid interference from the more mobile mate-seeking males (DANGERFIELD & TELFORD, 1992; TELFORD & DANGERFIELD, 1993a). In a small patch of *Acacia* savanna in Gaborone, Botswana (24°40'S, 25°52'E) there were significant differences between the sexes of three species in time spent walking, feeding, resting and copulating (Table 2, and see DANGERFIELD, MILNER & MATTHEWS, 1992).

Males tend to be the more mobile sex and invest most of their time searching the habitat for females. Females invest more time in feeding, probably to repay their significant energetic investment in ova.

PATTERNS

Mating patterns

Correlating variation in mating success with some measure of behaviour or morphology is the standard protocol for detecting patterns of non-random mating (e.g. PARTRIDGE & HALLIDAY, 1984). Non-random mating is assumed to be the consequence of some process of sexual competition in which individuals of superior competitive ability gain a mating advantage over rival conspecifics.

In a study of mating patterns in the Mazowe population of *Alloporus uncinatus* over a single breeding season (November 1988 - May 1989) mating was random with respect to body mass (g): unmated males (mean $\pm$ 1 s.e.) = 8.16 $\pm$ 1.08, n = 868; mated males = 8.24 $\pm$ 1.05, n = 295. MANN-WHITNEY U-test: U = -1.2, P>0.1, and see Fig. 2 in TELFORD & DANGERFIELD (1993a). A lack of any significant correlations between various measures of the body sizes (mass, length, width, head width) of males and females in copula pairs supported this conclusion (see Fig. 1). However, this evidence for random mating is not conclusive as the sampling protocol did not take into account the mating histories of individuals over the duration of the breeding season. This highlights the problems of studying mating success in natural populations of small, highly abundant, inconspicuous organisms. The focus of such studies must be at the level of the individual and requires the use of effective, reliable marking techniques.

The operational sex ratio

Another powerful predictor of local mate competition is the operational sex ratio (OSR), which is the ratio of sexually receptive males to females (EMLEN & ORING, 1977). Under male biased OSR conditions males are limited in their access to females and must compete for females as a limiting resource. The reverse is true under female biased OSR conditions.

Savanna millipede communities are characterized by large-scale temporal variation, and sex differences, in emergence and activity patterns (DANGERFIELD & TELFORD, 1991; DANGERFIELD, MILNER & MATTHEWS, 1992) with the nett effect of changing OSR conditions over the breeding season.
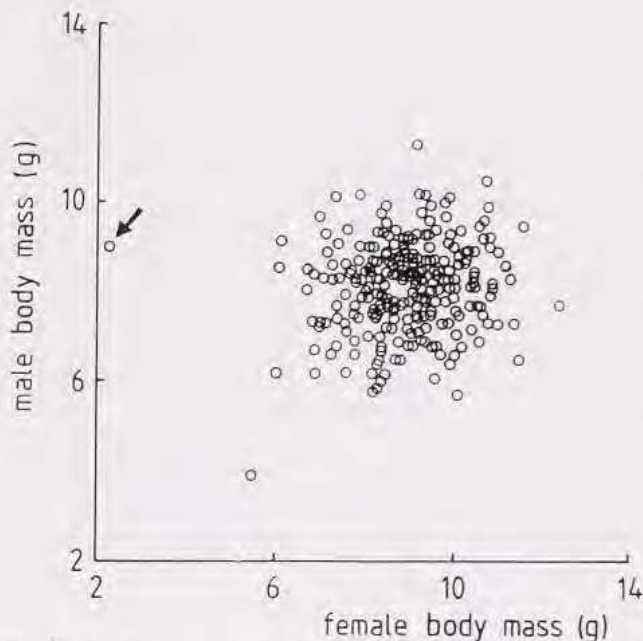
FIG. 1. — The relationship between body mass (g) of males and females in all mated pairs of *Alloporus uncinatus* collected over a single breeding season. Arrow indicates a pair in which the female received a fatal injury. Source: TELFORD & DANGERFIELD, 1993a.
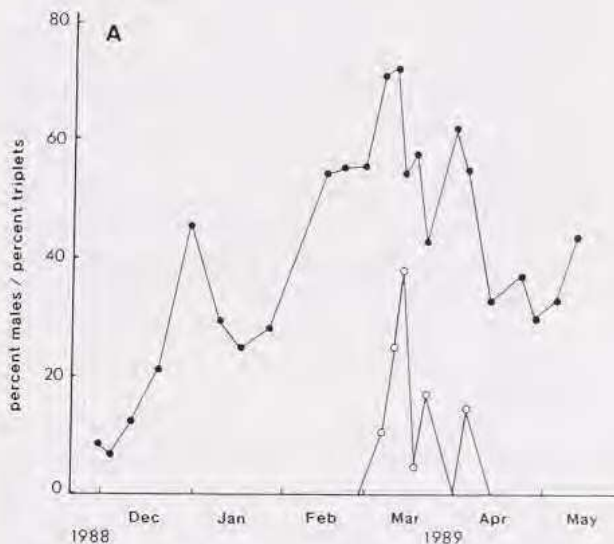

FIG. 2a. — Seasonal change in the operational sex ratio (●) and the occurrence of triplet associations as a proportion of the number of mated pairs (○) for the Mazowe population of *Alloporus uncinatus*. Source: modified from TELFORD & DANGERFIELD, 1993a.

The magnitude and timing of change in the OSR varies between populations and is also dependent on the duration of the breeding season. For example, in the Mazowe population of *A. uncinatus* the OSR was female biased at the onset of breeding. This bias gradually declined, ending in a peak of male bias coincident with the major peak in mating activity and the appearance of an alternative male mating tactic (Fig. 2a, and see TELFORD & DANGERFIELD, 1993a). This process of change in the OSR is a consequence of the presence of large numbers of intercalary males early in the season, and the gradual decline in number of mature females who presumably burrowed back into the soil to lay egg clutches.

Botswana populations of *A. uncinatus, Calostreptus carinatus* and *Chaleponcus digitatus* showed similar though less predictable change in the OSR (Fig. 2b). In a millipede community at Richards Bay, Natal (28°37'E, 32°17'S) females of the dominant species *Chersastus sanguinipes* were present constantly, but males only appeared immediately after a rainfall event, stayed for 2-3 days and then disappeared. Copula pairs were only observed during the times when males were present (Rudi VAN AARDE, pers. comm.).

In millipede breeding populations, the co-occurrence of alternative male mating tactics is a common observation under male biased OSR conditions. Instead of always searching for single females, males often joined copula pairs to form triplet associations. This observation will be discussed further in the following section.

PROCESSES

Mating experiments

Separating the effects of male-male competition from female choice remains one of the major challenges to students of sexual selection (see for example, KIRKPATRICK, 1982; ARNOLD, 1983; PARTRIDGE, 1983). Previously we argued that our field data on mating patterns were insufficient to refute
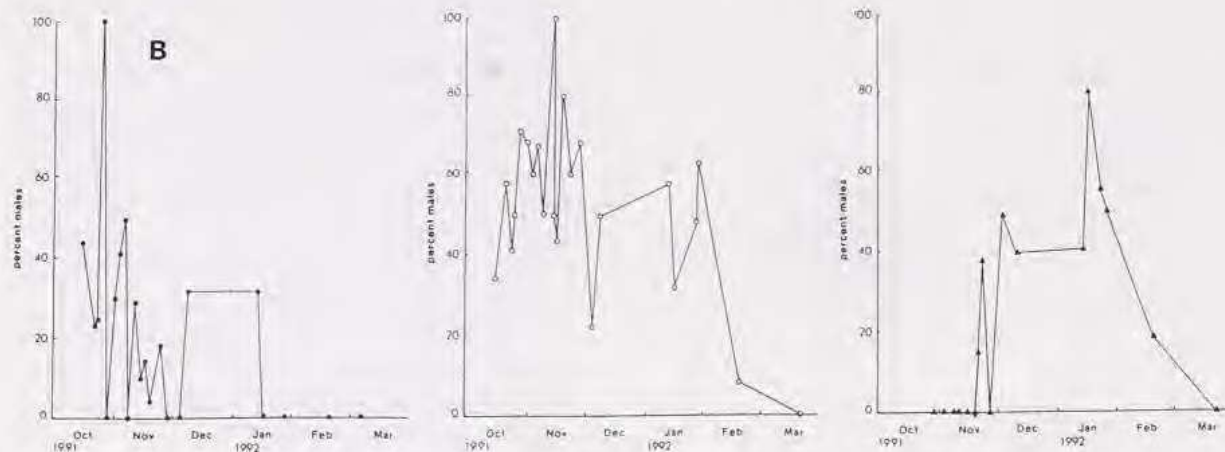
the occurrence of non-random mating.

FIG. 2b. — Seasonal change in the OSR for Botswana populations of *Alloporus uncinatus* (•) *Calostreptus carinatus* (▲) and *Chaleponcus digitatus* (○).
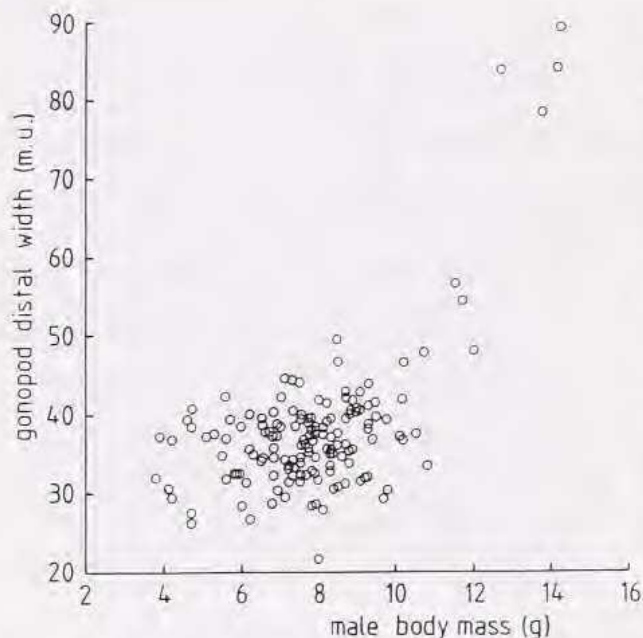

FIG. 3. — The relationship between body mass (g) and gonopod distal width for a sample of male *Alloporus uncinatus* from Mazowe.

Here we summarise results from controlled laboratory mating experiments designed to test for size assortative and size selective mating, and separate the effects of inter and intra-sexual selection in generating these mating patterns (TELFORD & DANGERFIELD, 1993b). Sequential choice experiments were conducted with *Alloporus uncinatus, Calostreptus carinatus, Spinotarsus tenuis, Chaleponcus digitatus* and *Chaleponcus limbatus*. Individual male and female mating histories for *A. uncinatus* from Mazowe (Fig. 3) and the two species of *Chaleponcus* revealed that, in the absence of a choice situation, mating was size selective (Table 3) and best explained by female choice (TELFORD & DANGERFIELD, 1993a, b). In the other species and populations mating was random.

In multiple choice mating experiments a wide variety of outcomes were observed (Table 4) including size assortative and random mating, and a mating advantage for both large and small males. In addition, between population comparisons of mating pattern were not always consistent. Our results suggest that both processes of sexual competition operate in millipede mating systems but do not always correspond for geographically separate populations of the same species (Table 5). These results should viewed as a source of testable *a priori* predictions about between-species and between-population differences in the competitive processes that generated these observed mating patterns.

TABLE 3. — Regression statistics for the relationship between frequency of acceptance and male body mass (g) for males in sequential choice mating experiments. Source: TELFORD & DANGERFIELD (1993b).

Species	Population	Sample size	Regression statistics		
			intercept	slope	r
A. uncinatus	Mazowe	245	-6.10	0.77	0.503***
	Hwange	22	-0.43	0.49	0.212ns
Calostreptus carinatus	Hwange	28	2.50	0.78	0.054ns
	Sengwa	39	1.93	1.48	0.095ns
Chaleponcus limbatus	V. Falls	35	-5.54	8.60	0.500**
	Marondera	25	-5.43	5.14	0.677***
Chaleponcus digitatus	Marondera	19	-8.77	8.77	0.583**
Spinotarsus	Marondera	16	2.06	0.42	0.001ns

TABLE 4. — Acceptance by females of first, second and third rank males as first and second mating partners in multiple choice mating experiments and the proportion of females that accepted a second male (PA). Source: modified from TELFORD & DANGERFIELD (1993b).

Species	Population		1st rank males	2nd rank males	3rd rank males	χ^2	PA
A. uncinatus	Mazowe	1st	15	7	3	7.85*	
		2nd	0	0	0	na	0
		2nd	6	2	4	2.00ns	48
Calostreptus carinatus	Hwange	1st	2	5	3	1.40ns	
		2nd	2	0	2	2.00ns	40
	Sengwa	1st	4	1	8	5.60*	
		2nd	2	1	3	1.00ns	46
Chaleponcus limbatus	V. Falls	1st	6	4	3	1.08ns	
		2nd	0	0	0	na	0
	Marondera	1st	7	2	1	6.19*	
		2nd	0	0	0	na	0
Chaleponcus digitatus	Marondera	1st	11	34		6.37*	
		2nd	4	1	5	2.48ns	50
Spinotarsus tenuis	Marondera	1st	7	1	1	8.00**	
		2nd	1	2	0	1.00ns	33
Spinotarsus cuspidosus	Marondera	1st	9	40		9.39**	
		2nd	0	0	0	na	0

MATING TACTICS

Intrasexual competition

Observations of courtship and copulation as well as mate seeking behaviour in both the field and laboratory provide further insight into the tactics of mate acquisition and processes of sexual competition employed by millipedes. Competition between males can be both direct and indirect. The primary mating tactic appears to be a scramble for mates in which males seek females through a random search of the habitat (TELFORD & DANGERFIELD, 1993a). When conspecifics are encountered males attempt copulation and tend to be indiscriminate. Interindividual differences in time spent searching and speed of movement may generate variance in male mating success and is, therefore, a form of indirect competition. Under male biased OSR conditions single males often join with copula pairs to form triplet associations (Fig. 2a, and see TELFORD & DANGERFIELD, 1990, 1993a) and either wait for the pair to separate before attempting to mate with the female (Spirostreptidae) or actively attempt to displace the copulating male (Odontopygidae). Attempted displacement of copulating males is a common mating tactic in invertebrate and anuran mating systems (THORNHILL & ALCOCK, 1983; LAMB, 1984; TELFORD & VAN SICKLE, 1990) and is a form of direct male competition.

Why males switch from searching for single females to associating with copula pairs when the OSR is male biased is an interesting unanswered question. We suggest that this change in behaviour does not reflect inferior competitive ability; as is the case for males of many species that perform alternative mating tactics (KREBS & DAVIES, 1987). A more parsimonious explanation is that as the OSR becomes increasingly male biased, encounter frequency with solitary females declines. Males then simply associate with the first female they meet regardless of whether she is paired or alone. This behaviour is "tolerated" by copulating males because they would have to release the female in order to repel the other male. One reason for this apparent tolerance of copulating males is because the physical nature of copulation (TELFORD & WEBB, in prep.) together with its long duration under male control (TELFORD & DANGERFIELD, 1993b, c) creates a potential sexual conflict of interest in which the male stands to gain more than the female.

Prolonged copulation is advantageous for males because it protects their reproductive investment in females under conditions of intense intrasexual competition (TELFORD & DANGERFIELD, 1991). The potential evolutionary benefits to females are less obvious (see THORNHILL & ALCOCK, 1983). Females can incur physical damage during copulation (see Fig. 1) which may be compounded through multiple mating (see for example, FOWLER & PARTRIDGE, 1989). Therefore, if a male releases a female to repel a rival male she may become unwilling to resume copulation. However, this still begs the question of why females remate with the second male in triplet associations. While the evolutionary benefits a male enjoys from multiple mating are obvious and well documented the same is not true for females (THORNHILL & ALCOCK, 1983). An often argued potential benefit of multiple mating by females is the increased heterozygosity in their offspring; this prediction still lacks empirical verification.

Copulation in spirostreptid millipedes occurs either in parallel (*Calostreptus*), head to head (*Rhodesiostreptus matabele*), or with the male coiled around the female (TELFORD & DANGERFIELD, 1990, 1993b). Interestingly, parallel copulators tend to mate for a shorter time period than coiled copulators. *Chaleponcus* sp. has the shortest copulation duration for a coiled copulator and single males of this species actively attempt to displace copulating males. However, attempted displacement has never been observed in parallel copulators which also typically perform short duration copulations. The significance of between species variation in copulation duration remains unclear, and definately warrants further study. Data on copulation

position, duration and displacement, copulatory guarding, and triplet formation are summarised in Table 6.

TABLE 5. — Predictions of expected mating patterns and processes of sexual competition in the mating systems of nine populations of spirostreptid millipede. Predictions are based on results obtained from sequential and multiple choice mating experiments (tables 3 & 4). * Small male mating advantage. ♂-♂ Comp.= male-male competition.

Species	Population	Sequential Choice		Multiple Choice	
		Pattern	Process	Pattern	Process
A. uncinatus	Mazowe	Size-Selective	♀ Choice	Size-Selective	♀ Choice ♂-♂ Comp.
	Hwange	Random	-	Size-Assortative	♀ Choice
Calostreptus carinatus	Hwange	Random	-	Size-Assortative	♀ Choice
	Sengwa	Random	-	Size-Selective*	♀ Choice
Chaleponcus limbatus	V. Falls	Size-Selective	♀ Choice	Random	-
	Marondera	Size-Selective	♀ Choice	Size-Selective	♀ Choice ♂-♂ Comp.
Chaleponcus digitatus	Marondera	Size-Selective	♀ Choice	Size-Selective	♀ Choice ♂-♂ Comp.
Spinotarsus tenuis	Marondera	Random	-	Size-Selective	♀ Choice ♂-♂ Comp.
Spinotarsus cuspidosus	Marondera	-	-	Size-Selective	♀ Choice ♂-♂ Comp.

Prolonged copulation in invertebrates appears to have evolved as a form of mate guarding in which males protect their reproductive investment in females by limiting their opportunity to remate (see THORNHILL & ALCOCK, 1983). In *Alloporus uncinatus*, males alter the duration of copulation according to predictions of the mate-guarding hypothesis (TELFORD & DANGERFIELD, 1993 b, c). Sperm competition (*sensu* PARKER, 1970) is the most likely process responsible for selection favouring the evolution of this form of mate guarding by males. This may also be true for other species of millipede with prolonged copulation (see Table 6).

Intersexual competition

In some invertebrates, primary or accessory genitalia scale positively with body size (EBERHARD, 1985; unpublished data for eight species of spirostreptid millipedes). In libellulid dragonflies, the hook-like structures at the end of the penis scale positively with body size and both size and degree of symmetry correlate with sperm volumes removed (MILLER, 1991). EBERHARD (1985) has suggested that females could use such a scaling relationship as a cue to male body size and use the information to choose large males as mates. We have already suggested that female choice may partially explain the mating advantage enjoyed by large males

of several species in sequential and multiple choice mating experiments (Table 5). However, invoking genitalic scaling as the mechanism of female choice may be incorrect.

For example, although the gonopods of *A. uncinatus* scale positively with body size (Fig. 3), the sizes of males and females in copula pairs from Mazowe do not correlate. If females do choose males on this basis then we would predict a positive relationship between the size of mating partners, or a correlation between mating success and body size in natural populations. To more fully understand this potential mechanism of female choice requires a systematic study of the ultrastructure of male and female genitalia (see BARNETT & TELFORD, this volume) together with a study of mating patterns in populations of known individuals.

TABLE 6. — Copulation duration in minutes (mean ± 1 s.d.) for eight populations of spirostreptid millipede (sample sizes are given in brackets). Copula positions are given below species names. Source: modified from TELFORD & DANGERFIELD (1993b), and unpublished data.

Family / Species	Population	Copulation duration	Triplets (Y/N)	Displacement (Y/N)
Spirostreptidae				
Alloporus uncinatus (coiled)	Mazowe	122.7 ± 49.4 (35)	Y	N
	Hwange	205.8 ± 60.8 (25)	Y	N
Calostreptus sp. (parallel)	Hwange	60.3 ± 25.6 (22)	N	N
	Sengwa	33.8 ± 22.9 (25)	N	N
Odontopygidae				
Chaleponcus sp.1 (coiled)	Marondera	22.6 ± 17.9 (40)	Y	Y
Chaleponcus sp.3 (coiled)	V. Falls	80.2 ± 25.3 (20)	Y	Y
	Marondera	85.6 ± 16.6 (19)	Y	Y
Chaleponcus digitatus (coiled)	Marondera	66.0 ± 11.2 (28)	Y	N
Spinotarsus tenuis (coiled)	Marondera	92.3 ± 18.6 (19)	Y	?

CONCLUSIONS

Millipedes are a conspicuous group of organisms, present in a wide variety of habitats and typically occurring at high population densities. They adapt well to laboratory conditions and are useful subjects for experimental manipulation.

Our study of the mating system of *Alloporus uncinatus* over a single breeding season revealed the nature of male mating tactics, the impact of change in the OSR on male mating tactics, and the role of stochasticity in generating the observed mating pattern. Our comparative data from laboratory mating experiments suggests that both male competition and female choice shape mating systems and that the relative roles of the two processes can differ between populations of the same species. Between population plasticity in mating systems is believed to be a consequence of the combined effects of environmental variability, differing population densities and operational sex ratios. Together, these results and predictions can be used to generate *a priori* hypotheses about plasticity in millipede mating systems, testable through detailed longitudinal studies of natural populations.

Descriptive studies, for example between species variation in the duration of copulation, are a necessary starting point for the investigation of the adaptive significance of any behaviour pattern. We have shown experimentally, that in *A. uncinatus* prolonging the duration of copulation is a form of mate guarding (TELFORD & DANGERFIELD, 1991) and our comparative data allow us to make similar predictions for other species. Where copulation duration is not prolonged the mate guarding explanation does not hold but nevertheless makes way for alternative *a priori* predictions to be made. For example, if copulation duration is short it may be because female remating frequency is low. Therefore, selection to guard females is relaxed and a better tactic for males is to reduce time spent in copula and maximise mating frequency.

The data presented here confirm the polygynandrous nature of savanna millipedes which, together with the capacity of females to store sperm and the functional role of gonopods in sperm displacement (BARNETT & TELFORD, this volume), highlight the importance of sperm competition in millipede mating systems. Quantifying sperm precedence patterns is essential to a complete understanding of the relative contributions of different processes of sexual competition to observable variation in male and female mating success.

REFERENCES

ALEXANDER, R. D., HOOGLAND, J. L., HOWARD, R. D., NOONAN, K. M. & SHERMAN, P. W., 1979. — Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. *In* : N. A. CHAGNON & W. IRONS, *Evolutionary biology and human social behaviour: An anthropological perspective*. North Scituate.

ARNOLD, S. J., 1983. — Sexual selection: The interface of theory and empiricism. *In* : P. BATESON, *Mate Choice* . Cambridge, Cambridge University Press : 67-108.

BARNETT, M., TELFORD, S. R. & DE VILLIERS, C. J., 1993. — Sperm displacement in a millipede? - an investigation into the genital morphology of the southern African Spirostreptid millipede *Orthoporus pyrhocephalus. J. Zool. Lond.*, 3 : 511.

BATEMAN, A. J., 1948. — Intrasexual selection in *Drosophila. Heredity*, 2 : 349-368.

BIRKHEAD, T. R., 1989. — The intelligent sperm? A concise review of sperm competition. *J. Zool. Lond.*, 218 : 347-351.

BIRKHEAD, T. R. & HUNTER, F. M., 1990. — Mechanisms of sperm competition. *Trends Ecol. Evol.*, 5 : 48-52.

BOAKE, C. R. B., 1986. — A method for testing adaptive hypotheses of mate choice. *Am. Nat.*, 127 : 654-666.

BORGIA, G., 1979. — Sexual selection and the evolution of mating systems. *In*: N. S. BLUM & M. A. BLUM, *Sexual selection and reproductive competition in insects*. New York, Academic Press.

BLOWER, J. G., 1985. — Millipedes. [*In* : D. M. KERMACH & R. S. K. BARNES, *Synopses of the British Fauna.*, 35], London, E. J. Brill. & W. Backhuys, 242 pp.

BROWN, D., 1988. — Components of Lifetime Reproductive Success. *In* : T. H. CLUTTON BROCK, *Reproductive Success*. Chicago, University of Chicago Press : 439-453.

CLUTTON BROCK, T. H., 1988. — Reproductive Success. In: T. H. CLUTTON BROCK, *Reproductive Success*. Chicago, University of Chicago Press : 472-485.

DANGERFIELD, J. M. & TELFORD, S. R., 1991. — Seasonal activity patterns of Julid millipedes in Zimbabwe. *J. Trop. Ecol.*, 7 : 281-285.

DANGERFIELD, J. M. & TELFORD, S. R., 1992. — Species diversity of Juliform millipedes: Between habitat comparisons within the seasonal tropics. *Pedobiologia* , 36 : 321-329.

DANGERFIELD, J. M., MILNER, A. E. & MATTHEWS, R., 1992. — Seasonal activity patterns and behaviour of juliform millipedes in south-eastern Botswana. *J. Trop. Ecol.*, 8 : 451-464.

DARWIN, C., 1871. — *The descent of man and selection in relation to sex*. London, John Murray.

EBERHARD, W. G., 1985. — *Sexual selection and animal genitalia*. Cambridge: Harvard University Press.

EMLEN, S. T. & ORING, L. W., 1977. — Ecology, sexual selection and the evolution of mating systems. *Science* , 197 : 215-223.

FOWLER, K. & PARTRIDGE, L., 1989. — A cost of mating in female fruitflies. *Nature* , 338 : 760-761.

GRAFEN, A., 1988. — On the uses of Data on Lifetime Reproductive Success. *In* : T. H. CLUTTON BROCK, *Reproductive Success*.. Chicago, University of Chicago Press : 454-471.

GOMENDIO, M. & ROLDAN, E. R. S., 1993. — Mechanisms of sperm competition: Linking physiology and behavioural ecology. *Trends Ecol. Evol.*, 8 : 95-100.

HOPKIN, S. P. & READ, H. J., 1992. — *The biology of millipedes.* Oxford, Oxford Univ. Press, 233 pp.

KIRKPATRICK, M., 1982. — Sexual selection and the evolution of female choice. *Evolution*, **36** : 1-12.

KREBS, J. R. & DAVIES, N. B., 1987. — *An introduction to behavioural ecology.* Oxford, Blackwell Scientific Publications.

LAMB, T., 1984. — Amplexus displacement in the southern toad *Bufo terrestris. Copeia* : 1023-1025.

MILLER, P. L., 1991. — The structure and function of the genitalia in the Libellulidae (Odonata). *Zool. J. Linn. Soc.*, **102** : 43-73.

PARKER, G. A., 1970. — Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.*, **45** : 525-567.

PARTRIDGE, L., 1983. — Non random mating and offspring fitness. *In* : P. BATESON, *Mate Choice.* Cambridge, Cambridge University Press : 67-108.

PARTRIDGE, L. & HALLIDAY, T. R., 1984. — Mating patterns and mate choice. *In* : J. R. KREBS & N. B. DAVIES, *Behavioural ecology: An evolutionary approach.* Oxford, Blackwell Scientific Publications : 222-250.

TELFORD, S. R. & DANGERFIELD, J. M., 1990. — Sex in millipedes: laboratory experiments on sexual selection. *J. Biol. Ed.*, **24** : 233-238.

TELFORD, S. R. & DANGERFIELD, J. M., 1991. — Sex ratio manipulation and copulation duration in the tropical millipede, *Alloporus uncinatus*: A test of the copulatory guarding hypothesis. *Anim. Behav.*, **40** : 984-986.

TELFORD, S. R. & DANGERFIELD, J. M., 1993a. — Mating tactics in the tropical millipede *Alloporus uncinatus* (Diplopoda; Spirostreptidae). *Behaviour*, 124 : 45-57.

TELFORD, S. R. & DANGERFIELD, J. M., 1993b. — Mating behaviour and mate choice experiments in some tropical millipedes (Diplopoda: Spirostreptidae). *S. A. J. Zool.*, **28** :155.

TELFORD, S. R. & DANGERFIELD, J. M., 1993c. — Males control the duration of copulation in the tropical millipede, *Alloporus uncinatus. S. A. J. Zool.*, 29 : 266.

TELFORD, S. R. & VAN SICKLE, J., 1989. — Sexual selection in an African toad (*Bufo gutteralis*): The roles of morphology, amplexus displacement and chorus participation. *Behaviour*, **110** : 62-75.

THORNHILL, R. & ALCOCK, J. 1983. — *The evolution of insect mating systems.* Cambridge, Massachusetts, Harvard University Press.

TRIVERS, R. L., 1972. — Parental investment and sexual selection. *In* : B. CAMPBELL, *Sexual Selection and the Descent of Man.* Chicago, Aldine : 136-179.

WAAGE, J. K., 1986. — Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biol. J. Linn. Soc.*, **28** : 285-300.

WALKER, W. F., 1980. — Sperm utilisation strategies in nonsocial insects. *Am. Nat.*, **115** : 780-799.

WILLIAMS, G. C., 1966. — *Adaptation and Natural Selection.* Princeton, NJ, Princeton University Press.